research to have an impact for good. I have spent the last 20 years studying the hormonal regulation of root growth and development, identifying several of the key signals, genes and regulatory networks that control root length, angle and branching in the model plant *Arabidopsis.* I recently started BBSRC and ERC research fellowships to manipulate water and nutrient uptake efficiency in crops — important traits that are controlled in large part by their root systems' architecture. My ambition is to exploit the knowledge I have accrued over the last two decades in *Arabidopsis,* to improve root development in crops.

Do you have a scientific role model? Professor Jonathan Lynch (Penn State) has been an important role model. He has pioneered, both in concept and practice, the idea of 'a second green revolution'. This concept focuses on improving root system architecture to optimize water and nutrient uptake in a sustainable manner; contrasting the original 'green revolution', which developed dwarf varieties responding to high fertilizer inputs. In practice, this involves screening bean or soybean seedlings for altered root phenotypes, such as root angle and root hair length. Field trial results on these new varieties grown in low-phosphate soils have been impressive, but the greatest improvements in phosphate uptake (<300%) have occurred by combining both root traits. These varieties have been integrated into bean and maize breeding programs at international centers such as CIAT and then released in South America, Africa and Asia where they are helping hundreds of thousands of farmers to significantly improve yields in low phosphate soils. Now that's what I call scientific impact!

What do you think are the big questions and challenges to be answered next in your field? Over recent decades, we have gained detailed knowledge of many processes involved in root growth and development. However, with this knowledge comes increased complexity and a pressing need for mechanistic modeling, to understand how these individual processes interact. One major challenge is in relating genotype to phenotype, requiring us to move beyond the gene and network scale to use multiscale modeling to predict emergent dynamics at the tissue and organ levels. This requires information about the key gene regulatory networks, cell and tissue geometries, mechanics and hydraulics. Whilst challenging, it is clear that multiscale models are set to become increasingly important to researchers if we are to bridge the 'genotype to phenotype gap'.

Developing a mechanistic model of a whole plant represents a logical next step. Indeed, given the exchange of water, nutrients and signals between root and shoot organs, developing a virtual root or shoot model in isolation could be considered naïve. Ultimately, plant performance is measured by breeders at the population scale, rather than individual. Hence, mechanistic multiscale models need to be developed that bridge the remaining physical scale between the plant and field to ensure that we are able to relate genotype to phenotype and aid attempts to reengineer key crop traits.

Phenotype represents the output of the interaction between genotype and environment. A major future challenge will be to develop mixed genetic eco-physiological models that capture genetic and environmental regulation. Environmental factors include physical properties of the soil, microbes, water availability, nitrogen distribution, macro/micro elements and competition with other root systems. X-ray micro CT has the potential to provide rich image data sets, enabling measurements of many of these root and soil parameters. Nevertheless, new methodologies to assay other soil properties such as nutrient distribution are also required. Armed with such information, we will be well placed to bridge the genotype–phenotype gap and parameterize predictive models designed to optimize crop root architectures for soil types and nutrient regimes. To address these challenging goals, I am working as part of a multidisciplinary team of researchers at CPIB composed of computer, plant and soil scientists, biophysicists, crop physiologists, engineers, statisticians and mathematicians. Working with such a team often takes me out of my comfort zone, but I am happy to do so as I truly believe that the major breakthroughs in biology in the coming decades will arise from working at the interface between disciplines.

Plant Sciences Division, School of Biosciences, University of Nottingham, Lougborough, LE12 5RD, UK.
E-mail: malcolm.bennett@nottingham.ac.uk

Quick guides

Tenrecs

Link E. Olson

What is a tenrec? Tenrecs are small to medium-sized (2–2,000 grams) placental mammals found in Madagascar and tropical Africa that are notable both for their purported primitiveness and their numerous unique specializations, an apparent contradiction which, along with other recent discoveries, has contributed to a resurgent interest in all aspects of tenrec biology. Their uniqueness was so apparent to European scientists that, not long after the first species was formally described in 1777, a new taxonomic family, Tenrecidae, was named to accommodate them. For the next two centuries, scientists would puzzle over how tenrecs are related to other placental mammals, with little consensus but no shortage of debate.

How many species of tenrecs are there? Today, 34 living species are recognized, all but three of which are endemic to the island continent of Madagascar (that is, they are found nowhere else). The African species are divided into two genera and are collectively, albeit erroneously, called otter shrews. This double misnomer — they are neither otters nor shrews — refers to their semiaquatic adaptations and superficial similarity to small-bodied otters. (The word 'shrew' is used in combination with other words in the common names of many mammal species, usually in reference to their shrew-like diet or appearance; *true* shrews comprise their own family, Soricidae.) Otter shrews are extremely elusive and therefore poorly studied; this is particularly true of the two dwarf otter shrews in the genus *Micropotamogale*.

The remaining 31 tenrec species occur naturally only on Madagascar. One species, the tail-less tenrec *Tenrec ecaudatus* (Figure 1), has been successfully introduced to other islands in the eastern Indian Ocean, including Réunion, Mauritius, the Seychelles, and the Comoros. Nearly one-third of Malagasy tenrec species have been described in the past two decades alone, and tenrec experts

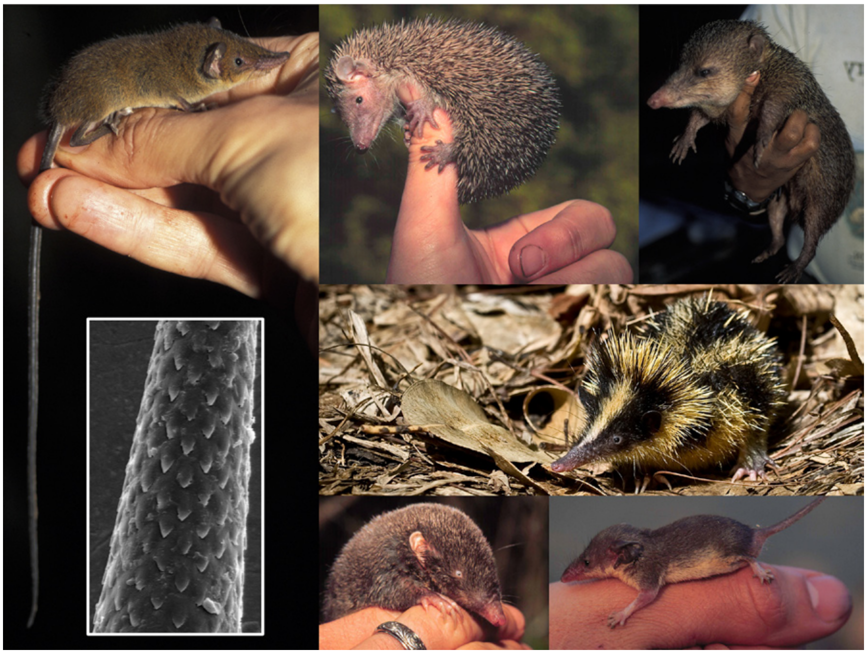

Figure 1. Tenrec evolution run amok.
Clockwise from upper left: lesser long-tailed shrew tenrec; lesser hedgehog tenrec; tail-less tenrec; lowland streaked tenrec; large-eared tenrec; mole-like rice tenrec; and barbed spine of a highland streaked tenrec. Photos by Link E. Olson and Jonathan L. Fiely.

suspect many more remain to be discovered.

Why so many new species? In addition to tenrecs, new species of rodents, carnivores, bats, and lemurs have been described from Madagascar in the past five years alone. In some cases, species that were first described long ago based on a small number of specimens (often only one) were later deemed insufficiently distinct from a previously described species and lumped back into the first species. A resurgence of biological exploration on Madagascar in the last quarter century has resulted in the collection of additional specimens of many synonymized species, often leading to their resurrection in the light of new comparative material. These same expeditions frequently yield unidentifiable specimens that form the basis of new species descriptions. Genetic and, increasingly, genomic data often feature prominently in both scenarios, with several recent studies comparing the DNA from museum specimens collected over a century ago to the same genetic markers in recently captured individuals. Other technological and methodological advances allow today's scientists to study morphological and behavioral differences that were essentially undetectable a century, and in some cases even a decade, ago.

Why are tenrecs so interesting to evolutionary biologists? Tenrecs are believed to have evolved from a single species that somehow colonized Madagascar from Africa between 42 and 25 million years ago. Then, as now, Madagascar was separated from southeastern Africa by the Mozambique Channel, currently 230 km (143 miles) across at its narrowest point and a formidable biogeographic barrier. Originally part of the southern supercontinent Gondwana, Madagascar became separated from other continental landmasses at a time when mammals as we know them today had not yet evolved. Despite the spectacular ensuing diversification of mammals on Africa and its geographic proximity to Madagascar, only six lineages of terrestrial mammals (not including bats) managed to establish themselves on the island. Two of these — hippos and a bizarre aardvark-like creature called *Plesiorycteropus* — are extinct on Madagascar and known only from fossils.

The remaining four groups, which include lemurs, carnivores, rodents and tenrecs, all underwent adaptive radiations, each from a single colonizing ancestor that arrived separately on Madagascar. How they reached Madagascar will forever remain a mystery, but the most likely explanation is that a small number of individuals, possibly even a single pregnant female, passively rafted on mats of floating vegetation washed or blown out to sea from Africa. The unlikelihood of such events over short timescales led famed 20th century paleontologist George Gaylord Simpson to term the phenomenon 'sweepstakes dispersal'. This scenario is not unique to mammals, or even animals; the stunning diversity and endemism of much of Madagascar's biota is due, at least in part, to its geological history and the underappreciated role played by chance.

Once established, Malagasy tenrecs seem to have run amok evolutionarily and diversified to occupy nearly every available habitat on Madagascar, with the greatest diversity found in the island's eastern humid forests. As with otter shrews, many Malagasy species have evolved superficial resemblances to more familiar but unrelated mammals not found on Madagascar. The two species of hedgehog tenrec (Figure 1), for example, look strikingly similar to — you guessed it — hedgehogs (family Erinaceidae), complete with a full coat of hardened spines and the ability to roll into an impenetrable ball when threatened. Spines of closely-related streaked tenrecs (*Hemicentetes* spp.) are barbed and detachable, much like those of New World porcupines (which are rodents). Both species of rice tenrecs (also called mole tenrecs) in the genus *Oryzorictes* are semifossorial (spend part of their lives underground) and share several similarities to moles in the family Talpidae, such as reduced eyes and ears, velvety fur, and enlarged front feet adapted to digging (Figure 1). And despite extensive variation in morphology, ecology, and behavior, all 22 species of shrew tenrecs in the genus *Microgale* do, in fact, bear some resemblance to shrews.

These and other examples of convergence, in which distantly-related species independently evolve similar solutions to similar problems, allow evolutionary biologists to study adaptation over long evolutionary timescales. Superficial similarities resulting from convergence often arise through very different genetic and/or developmental pathways. Hedgehog spines, for example, are composed of multiple individual hairs while those of hedgehog tenrecs consist of single modified hairs. The two taxa also use different muscles in a different configuration to roll into a defensive ball. (Despite this, the external differences between hedgehogs and hedgehog tenrecs are so subtle that the U.S. Department of Agriculture has banned the import of hedgehog tenrecs — popular in the exotic pet trade — into the U.S. in an attempt to control the spread of foot-and-mouth disease in livestock, not because tenrecs are known to transmit the disease but because *hedgehogs* are, and the risk of inadvertently importing an infected hedgehog masquerading as a hedgehog tenrec is deemed too great.) Examples of convergence can even be found within Tenrecidae. Madagascar's only semiaquatic tenrec, the web-footed tenrec (*Limnogale*), shares so many similar features with the African otter shrews that they were once thought to be more closely related to each other than to all other tenrecs; it is now widely accepted that *Limnogale* is instead a highly modified shrew tenrec that should perhaps be reclassified in the genus *Microgale*. The naked-nosed shrew tenrec, *Microgale gymnorhyncha*, appears to be incipiently fossorial and shares several adaptations to digging with *Oryzorictes*.

Malagasy tenrecs have also evolved many of their own unique adaptations, often going to extremes and pushing the boundaries of what it means to be a mammal. The large-eared tenrec (*Geogale aurita*), for example, is heterothermic over a broad range of temperatures; not using precious energy to maintain a constant body temperature may allow it to subsist on a relatively nutrient-poor diet of termites. Both species of streaked tenrecs possess a muscular 'stridulating' organ found in no other living mammal that, when activated, causes the quills on their lower back to rattle together extremely rapidly; the resulting high-pitched buzzing sound is used to communicate among individuals in a foraging group. Streaked tenrecs have also been shown to use a form of echolocation to navigate in the dark. The lowland streaked tenrec (*Hemicentetes semispinosus*) was once recognized by the Guinness Book of World Records as having the shortest generation time of any known mammal; females can become reproductively active at 25 days of age. Their closest relative, the tail-less tenrec, has been known to give birth to 32 young in a single litter, another record among mammals. Despite their diminutive size (7 grams on average), lesser long-tailed shrew tenrecs (*Microgale longicaudata*) can have up to 52 vertebrae in their tail (Figure 1), more than any other mammal alive or extinct, and may use their semi-prehensile tail as a fifth appendage to assist them in climbing branches and lianas. Future studies are sure to reveal additional evolutionary novelty in tenrecs.

What do tenrecs eat? Tenrecs are often referred to as insectivorous, but a more appropriate term is faunivorous, meaning they eat a diverse variety of animals (and not just insects). Most tenrecs eat terrestrial invertebrates, although several species will opportunistically eat other small vertebrates such as amphibians, reptiles, birds, rodents, and other tenrecs. Some species are known to eat carrion. Otter shrews and the web-footed tenrec specialize on aquatic prey, including crustaceans. Streaked tenrecs are thought to specialize on earthworms, which is consistent with their foraging behavior, long and slender snout, and extremely reduced teeth. Despite such seemingly similar diets, as many as 14 tenrec species have been recorded from the same locality, with up to 11 shrew tenrecs alone sharing the same habitat. How they partition prey within such an apparently crowded community of small-bodied faunivores remains unknown and has proven to be a challenging question to answer.

What eats tenrecs? Tenrecs are prey to many of Madagascar's native carnivores, raptors, snakes, and possibly other reptiles. Larger-bodied species, such as the tail-less and streaked tenrecs, are actively hunted as a food source for humans. Tail-less tenrecs are farmed for food on Réunion Island, a practice that may be spreading to other islands, including Madagascar. Hunting pressure on Madagascar is not known to be negatively impacting tenrec populations.

So how* do *tenrecs fit in the mammal tree of life? Tenrecs were long thought to share a common ancestor with the other major families of 'insectivorous' mammals, including shrews, moles, hedgehogs, solenodons (Solenodontidae), and golden moles (Chrysochloridae). For over a century, these six groups were placed in their own taxonomic order (variably Insectivora or Lipotyphla) and considered to collectively represent the most primitive and central branch of the placental mammal family tree. The problem with this arrangement was that no single feature or combination of features could be found to group them together to the exclusion of all other mammals. Indeed, the only thing they appeared to have in common was a shared *lack* of any features useful for grouping one or more of them with any other mammal family. Their simplified molars and premolars, given inordinate emphasis by traditional taxonomists and paleontologists, were seen as further evidence of their primitiveness (although the molars of insectivorous bats, tree-shrews, and elephant shrews closely resemble those of shrews and moles). Among the six insectivoran families, the teeth of tenrecs, golden moles, and solenodons are most similar to one another (the molars of the giant otter shrew, *Potamogale velox*, are curiously intermediate). Not surprisingly, solenodons (large-bodied faunivorous mammals found only on the Caribbean islands of Cuba and Hispaniola) and/or golden moles (exquisitely adapted small-bodied fossorial insectivores that swim through the sands of sub-Saharan Africa) were considered by many to be the closest relatives of tenrecs.

Imagine the surprise, then, when a steadily growing number of studies based on DNA sequence data starting in the late 1990s quickly converged on a most unexpected outcome. Although tenrecs and golden moles were, indeed, reconstructed as each other's closest relatives, they were found to be only distantly related to the other former insectivoran families. Instead, they appeared to share a common ancestor with a diverse menagerie of other seemingly unrelated mammals of African origin, including elephants, hyraxes, dugongs and manatees, elephant shrews, and aardvarks. Initially greeted with deep skepticism, if not outright disbelief, this assemblage — named Afrotheria — and its shared evolutionary history is now widely accepted, and an overwhelming amount of genomic data as well as numerous other lines of supportive evidence have since been adduced. Long regarded as unmodified primitive holdovers from an ancestral mammal stock, tenrecs are now regarded as the successful result of millions of years of evolutionary experimentation.

Is there anywhere I can I see a tenrec? Tenrecs, particularly tail-less and hedgehog tenrecs, can be found in many zoos. But the best place to see a tenrec is in Madagascar. A number of national parks and other protected areas staffed by trained Malagasy naturalists provide ecotourists with unprecedented opportunities to experience Madagascar's remarkable biodiversity.

Where can I learn more about tenrecs?

The Animal Diversity Web (http://animaldiversity.ummz.umich.edu/).
BBC Nature Wildlife (http://www.bbc.co.uk/nature/life/Tenrecidae).
Benstead, J.P. and Olson, L.E. (2003). *Limnogale mergulus*. In The Natural History of Madagascar, S.M. Goodman and J.P. Benstead, eds. (Chicago: University of Chicago Press), pp 1267–1273.
Eisenberg, J.F. and Gould, E. (1970). The Tenrecs: A Study in Mammalian Behavior and Evolution. (Washington, D.C.: Smithsonian Institution Press).
Goodman, S.M. (2003). *Oryzorictes*, mole tenrec or rice tenrec. In The Natural History of Madagascar, S.M. Goodman and J.P. Benstead, eds. (Chicago: University of Chicago Press), pp 1278–1281.
Jenkins, P.D. (2003). *Microgale*, shrew tenrecs. In The Natural History of Madagascar, S.M. Goodman and J.P. Benstead, eds. (Chicago: University of Chicago Press), pp 1273–1278.
Olson, L.E., and Goodman, S.M. (2003). Phylogeny and biogeography of the tenrecs. In The Natural History of Madagascar, S.M. Goodman and J.P. Benstead, eds. (Chicago: University of Chicago Press), pp 1235–1240.
Olson, L.E., Goodman, S.M., and Yoder, A.D. (2004). Illumination of cryptic species boundaries in long-tailed shrew tenrecs (Mammalia: Tenrecidae; *Microgale*): New insights into geographic variation and distributional constraints. Biol. J. Linn. Soc. *83*, 1–22.
Poux C., Madsen, O., Glos, J., de Jong, W.W., and Vences, M. (2008). Molecular phylogeny and divergence times of Malagasy tenrecs: influence of data partitioning and taxon sampling on dating analyses. BMC Evol. Biol. *8*, 102.

University of Alaska Museum, 907 Yukon Drive, Fairbanks, Alaska, 99775, USA.
E-mail: link.olson@alaska.edu

Drosophila suzukii

Omar Rota-Stabelli[1], Mark Blaxter[2], and Gianfranco Anfora[1]

What is* Drosophila suzukii*? Not just another *Drosophila* species. *D. suzukii* is an invasive, destructive crop pest that originated in South East Asia. The species is also known as Spotted Wing *Drosophila*, because, as in many other *Drosophila* species, males have one dark spot on each wing and two sex combs (Figure 1A). *D. suzukii* recently invaded western countries and is threatening both European and American fruit industries.

Why is* D. suzukii *a menace? Because it is extremely fond of otherwise undamaged, ripening fruits, unlike most other *Drosophila* species which attack only decaying or rotten fruits. *D. suzukii* uses a simple evolutionary advantage, a serrated ovipositor (Figure 1B), to pierce the relatively hard skin of fruits and lay eggs in them. The damage is caused by larvae feeding within the fruits, making them quite protein rich but useless for the market. What is worse is that *D. suzukii* is fond of virtually every small fruit: it will quite happily feast on grapes, pears, apples, tomatoes, peaches, apricots, and plums, although its favourites are cherries and berries. Direct crop loss is the major problem in the first year of invasion, with peaks of 80% reduction in yield. After the pest has become established, eradication is virtually impossible and costs of production rise permanently because of the requirement for monitoring, management, increased chemical inputs, and secondary selection of fruits. The fly is also a potential threat for the biodiversity and the ecology of the invaded areas.

When and how did it arrive in western countries? *D. suzukii* is endemic to Asia, where it is widely distributed in temperate climates from Japan to Pakistan. Its western invasion started in 2008 with three synchronous outbreaks in California, Spain, and Italy (Figure 1C). These first records were close to ports, suggesting that the first individuals arrived as eggs or larvae in fruits sea-traded from Asia. By the end of 2010, the outbreak had spread to the American East coast, Canada, and most of the Mediterranean basin. Latest reports show that the outbreak is escalating with new records announced monthly. The UK has been recently added to the list, and *D. suzukii* is now at the borders of Scandinavia. Few records are available from developing countries, though it is expected that the pest has also colonised additional territories. From an ecological point of view, this invasion has few precedents, and *D. suzukii* is quickly becoming a model for research on invasion biology and pest management (Dreves 2011, Cini *et al*. 2012).

***Why has* D. suzukii *been able to invade so quickly*?** There are several compelling reasons. The first is niche-filling: *D. suzukii* fits the western agricultural environment where there are virtually no competitors for fresh fruits, nor natural predators or parasitoids. Second, *D. suzukii* shows a series of adaptations to temperate climates, which allow it to overwinter, even high in the Alps or Canada where it regularly freezes. A third is the species' dispersal mode: *D. suzukii* can move quickly from a region to another, either flying or being passively introduced by the fruit trade. Last, *D. suzukii* has a high reproductive output: a single female can lay hundreds of eggs during her life, which develop through three larval instars into adults in just 10 days at room temperature. As there may be up to 10 generations a year, a single colonising female can generate billions of descendants by the end of her reproductive season.

What is being done to tackle* D. suzukii*? The first action was in the Americas: since 2010, a number of West coast Universities and Institutions have run a consortium funded by the US Department of Agriculture to monitor and control the spread of the fly. In Europe, various national institutions are monitoring the fly, and within the EU there are proposals to monitor and study *D. suzukii* at the continental level. To provide growers with immediate help, front-line monitoring and surveys have focused on traps and frequent pesticide application, in some cases hazardously close to